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Adapting management to a changing world: Warm temperatures, dry soil, and interannual variability limit restoration success of a dominant woody shrub in temperate drylands

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Abstract

Restoration and rehabilitation of native vegetation in dryland ecosystems, which encompass over 40% of terrestrial ecosystems, is a common challenge that continues to grow as wildfire and biological invasions transform dryland plant communities. The difficulty in part stems from low and variable precipitation, combined with limited understanding about how weather conditions influence restoration outcomes, and increasing recognition that one-time seeding approaches can fail if they do not occur during appropriate plant establishment conditions. The sagebrush biome, which once covered over 620,000 km^2 of western North America, is a prime example of a pressing dryland restoration challenge for which restoration success has been variable. We analyzed field data on *Artemisia tridentata* (big sagebrush) restoration collected at 771 plots in 177 wildfire sites across its western range, and used process-based ecohydrological modeling to identify factors leading to its establishment. Our results indicate big sagebrush occurrence is most strongly associated with relatively cool temperatures and wet soils in the first spring after seeding. In particular, the amount of winter snowpack, but not total precipitation, helped explain the availability of spring soil moisture and restoration success. We also find considerable interannual variability in the probability of sagebrush establishment. Adaptive management strategies that target seeding during cool, wet years or mitigate effects of variability through repeated seeding may improve the likelihood of successful restoration in dryland ecosystems. Given consistent projections of increasing temperatures, declining snowpack, and increasing weather variability throughout midlatitude drylands, weather-centric adaptive management approaches to restoration will be increasingly important for dryland restoration success.

KEYWORDS

adaptive management, *Artemisia tridentata*, big sagebrush, climate change, drylands, environmental variability, Great Basin, snowpack

1 | INTRODUCTION

Dryland ecosystems, which comprise over 40% of the earth's terrestrial ecosystems (Huang, Yu, Guan, Wang, & Guo, 2016), have seen dramatic shifts in plant community composition driven by a legacy of livestock grazing combined with increasing disturbances (e.g., wildfire, invasive species), human development, and changing climates (D'Antonio & Vitousek, 1992; Knick et al., 2011; Milton & Siegfried, 1994; Schlesinger et al., 1990). Loss of native plant communities and potential desertification in drylands has created widespread need for effective ecological restoration to restore and maintain productivity of rangelands, reestablish native plants, promote wildlife habitat, limit further expansion of invasive species, and reduce erosion. Restoration of native species and communities is challenging in drylands, where low and variable precipitation create conditions in which plant communities are typically less resilient to disturbance and require more intervention than just one-time seeding. The availability of surface soil moisture, thought to be critical for germination and survival of new recruits, can vary considerably from year-to-year (Noy-Meir, 1973). As a result, recruitment can be infrequent and episodic even in undisturbed ecosystems (Andrus, Harvey, Rodman, Hart, & Veblen, 2018; Maier, Perryman, Olson, & Hild, 2001; Petrie et al., 2017; Schlaepfer, Lauenroth, & Bradford, 2014) and dryland restoration is often only marginally successful (e.g., Knutson et al., 2014).

There is increasing recognition that adapting restoration practices to variable environments could improve the likelihood of success in drylands (Hardegree et al., 2018). For example, identifying and quantifying environmental drivers that lead to successful plant establishment after seeding and the increasing skill of midrange weather forecasting (e.g., Kapnick et al., 2018) could allow managers to anticipate "good" years to increase success rates. Even in the absence of skillful multimonth predictions, understanding controls over regeneration could allow assessment of benefits of seeding over multiple years (Bradford, Betancourt, Munson, & Wood, 2018; Chambers et al., 2014; Davies, Boyd, Madsen, Kerby, & Hulet, 2018). Yet, most reported restoration outcomes typically focus on a handful of sites and rarely link observed restoration successes and failures to environmental conditions. Detailed understanding of the link between environmental conditions at the time of seeding and restoration outcomes can help resource managers to design and implement effective restoration strategies (e.g., Germino et al., in press).

The challenges of restoration across vast dryland landscapes are perhaps best typified by big sagebrush (*Artemisia tridentata*; hereafter sagebrush). Sagebrush is a dominant species of the sagebrush biome that once covered ~620,000 km^2 of western North America and provides habitat for many wildlife and plant species (Davies et al., 2011). However, sagebrush ecosystems have declined substantially as a result of positive feedbacks between wildfires and invasive annual grasses (most notably *Bromus tectorum*; Balch, Bradley, D'Antonio, & Gómez-Dans, 2013). It is now estimated that 50%–60% of historical sagebrush range now has exotic annual grasses as the primary overstory or understory species (West, 2000). Sagebrush is not fire-adapted; individuals do not resprout. Wildfire typically kills adult plants, before the current-year's reproduction, and kills surface seeds residing in seedbanks unless buried deep enough to maintain physiological dormancy and protect them from lethal temperatures (Wijayratne & Pyke, 2012). Nearly, 60% of the Great Basin is managed by the Bureau of Land Management (BLM), which reseeds sagebrush, other shrubs, perennial grasses, and forbs after wildfire with the goal of minimizing soil erosion, reducing invasive grasses, and restoring wildlife habitat (particularly for Greater sage grouse) (USDI BLM, 2007). Since 1990 the BLM has seeded at least 5,720 km^2 in the Great Basin with sagebrush seed, a total cost of at least 18.4 million for sagebrush seed alone (Pilliod & Welty, 2013). In much of the affected area, seeding rarely leads to appreciable recovery of sagebrush cover and density, and this has meant that goals of sage-grouse habitat recovery have largely not been achieved (Arkle et al., 2014; Knutson et al., 2014). When sagebrush does germinate, survival through the first year seems to be particularly limiting (Brabec et al., 2015). There are still considerable knowledge gaps about how climate and other variables influence establishment. Quantifying drivers of sagebrush establishment and recovery is an important step towards improving seeding outcomes.

Like most plants in temperate, arid ecosystems, aligning windows of soil moisture availability with suitable growing season temperatures is thought to be a critical driver of sagebrush recruitment (Brabec, Germino, & Richardson, 2017; Maier et al., 2001; Schlaepfer et al., 2014). But at larger spatial and temporal scales, the amount of precipitation has been found to be a weak predictor of sagebrush dynamics, and temperature often appears more dominant (Renwick et al., 2018; Tredennick et al., 2016). But, studies rarely consider the indirect effect temperature plays in driving patterns of plant available water in temperate regions through controlling snowpack and influencing soil moisture dynamics. Because snowmelt allows for increased water infiltration, limits evapotranspiration, and releases water later into the growing season, reduced snowpack may lead to less soil water availability even if the total precipitation remains constant (Loik, Breshears, Lauenroth, & Belnap, 2004). Earlier snowmelt can also expose recent germinates to extremely cold temperatures by moving up the critical window of soil moisture availability to colder periods in early spring (Brabec et al., 2017; Buma et al., 2017). The uncoupling of suitable temperature and moisture can result in a greater risk of water stress and frost exposure under warmer conditions, even if total precipitation is unchanged. Together this may help explain why sagebrush restoration is often least successful at low elevations (Davies et al., 2011; Knutson et al., 2014).

Here, we examine the impact of annual environmental conditions, including temperature, precipitation, snowpack, and soil moisture, on the success of sagebrush restoration after fire in the Great Basin of western North America. Big sagebrush plant communities in the Great Basin are expected to experience increased warming, declines in snowpack, and increased interannual variability in weather, including precipitation amount in the next century (Collins et al., 2013; Palmquist, Schlaepfer, Bradford, & Lauenroth, 2016a, 2016b). Using field data and process-based soil water modeling at 771 plots across the Great Basin, we examine whether environmental conditions at the time of seeding can help explain the likelihood of sagebrush occurrence at plots that were seeded after fire. Using these results, we then illustrate how seeding approaches can be adapted to maximize the likelihood of plant establishment in dryland ecosystems with increasing variability. Specifically, we pursue three objectives: (a) Identifying what environmental conditions are critical in driving sagebrush occurrence after seeding; (b) Quantifying the impact of these conditions on the probability of sagebrush occurrence; and (c) Predicting how adaptive management strategies (anticipatory seeding and multiyear seeding) could improve the probability of restoration success in the face of predicted climate change.

2 | MATERIALS AND METHODS

2.1 | Data collection

Within the Great Basin (Figure 1), we sampled 138 randomly selected wildfires from all known wildfires in the Land Treatment Digital Library (Pilliod & Welty, 2013) that burned between 1980 and 2014 and had been seeded subsequently with big sagebrush (a population of ~2,000 fires). At each wildfire site, we sampled up to five randomly located plots (average of 4.4 plots per site, n = 605 plots). Because our goal was to identify drivers of sagebrush occurrence, and successful sites can be comparatively uncommon (Knutson et al., 2014), BLM field offices were also asked to identify fires where they believed successful restoration had occurred (although sagebrush was not found in all upon sampling). These nonrandom fire sites (39 fire sites with up to 5 plots each) were included in all analyses except where noted (n = 166 plots; total random and nonrandom n = 771 plots). Fire sites often cover 10–100 km^2 and plots were frequently 200–400 vertical meters apart in elevation. As a result, plots within a fire site could in some cases be geographically closer to plots in another site than their own site, and span a significant portion of the total observed environmental conditions. Thus, we chose to perform all analyses at the level of plots.

At each plot, we quantified sagebrush occurrence (at least one sagebrush in the plot) or nonoccurrence (no sagebrush present) along three 50-m belt density transects (see Herrick, Van Zee, Havstad, Burkett, & Whitford, 2005). To maximize the likelihood of detecting sagebrush when present and to accurately and efficiently estimate density, the width of transect belts began at a maximum of 6 m but were sequentially reduced in size to 4, 2, and 1 m if observers initially expected to capture more than 20, 50, 70 individuals in the 6, 4, 2-m widths respectively. Field data were collected once per plot in 2011, 2014, 2015 or 2016. Times since seeding ranged from 1 to 35 years. Because our goal was to infer the drivers of sagebrush establishment in the growing season directly following seeding, we focus on sagebrush occurrence which is less likely to be influenced by subsequent years' survival and recruitment, rather than sagebrush density. Although we cannot fully eliminate the possibility of false-negative outcomes (establishment took place, but all established individuals died prior to sampling), high survival rates among larger sagebrush make this unlikely (Owens & Norton, 1990). Seeding years and polygons for the area seeded were identified using BLM records stored in the Land Treatment Digital Library (Pilliod & Welty, 2013). In 21% of cases, seeding occurred but the exact year was not known, in these cases seeding was assumed to have occurred before the first postfire growing season (i.e., by April). This was by far the most common time of seeding; 89% of plots with known seeding and fire years were seeded before the first postfire growing season.

2.2 | Ecohydrological modeling

To quantify ecohydrological conditions following fire, including effects of vegetation recovery on soil moisture, we simulated annual, plot-specific conditions in SoilWat2 (Version 3.2) (Bradford, Schlaepfer, Lauenroth, & Burke, 2014; Schlaepfer, Lauenroth, & Bradford, 2012a). SoilWat2 is a daily time-step, multiple soil layer, mechanistic model of ecosystem water balance that accounts for plot-specific interactions between climate, soil conditions, and vegetation, to estimate water pools and fluxes. Daily maximum and minimum temperatures and daily precipitation amounts were extracted from the University of Idaho Gridded Surface Meteorological Dataset for 1979–2016 at a resolution of 4-km (Abatzoglou, 2013). Soil texture properties needed for modeling were derived from field collected soil samples up to 50 cm deep when available and the remaining layers, up to 250 cm, were characterized using matching soil map unit components from the SSURGO national database (Soil Survey Staff 2017; See Supporting Information for depth specification of each layer).

Plant biomass and functional type are also key variables for quantifying the effect of vegetation on soil water availability in SoilWat2. We used line-point intercept (LPI) measurements of species cover conducted at the same time as sagebrush occurrence measurements to develop plant functional type (PFT) recovery endpoints for each plot (3 spoke-in-wheel transects, Herrick et al., 2005). Potential plant biomass at each plot was estimated using algorithms within SoilWat2 that account for the effect of temperature and preciptation on these factors (see Bradford et al., 2014). We then developed three postfire vegetation states to simulate vegetation recovery from fire using LPI data aggregated by PFT. Vegetation states were: (a) year 1 postfire – 10% annual plant cover, (b) years 2–5 postfire—present-day PFT composition at 10% of potential biomass, (c) years 6–10 postfire—present-day PFT composition at 50% of potential biomass (Bates et al., 2009; West & Hassan, 1985). We used vegetation recovery states in analyses identifying drivers of sagebrush occurrence (see Objective 1; seeding did not always occur the same year as fires) and simulations of repeated seeding after the *actual* initial seeding event (see Objective 3). In another analysis of interannual variability in sagebrush establishment probability, we used only the year 1 postfire vegetation state to calculate what sagebrush establishment probabilities *would* have been the year following fire, *if* the fire and seeding had occurred any one of the years from 1979 to 2016 (see Objective 3). However, overall, the impacts of vegetation states on soil

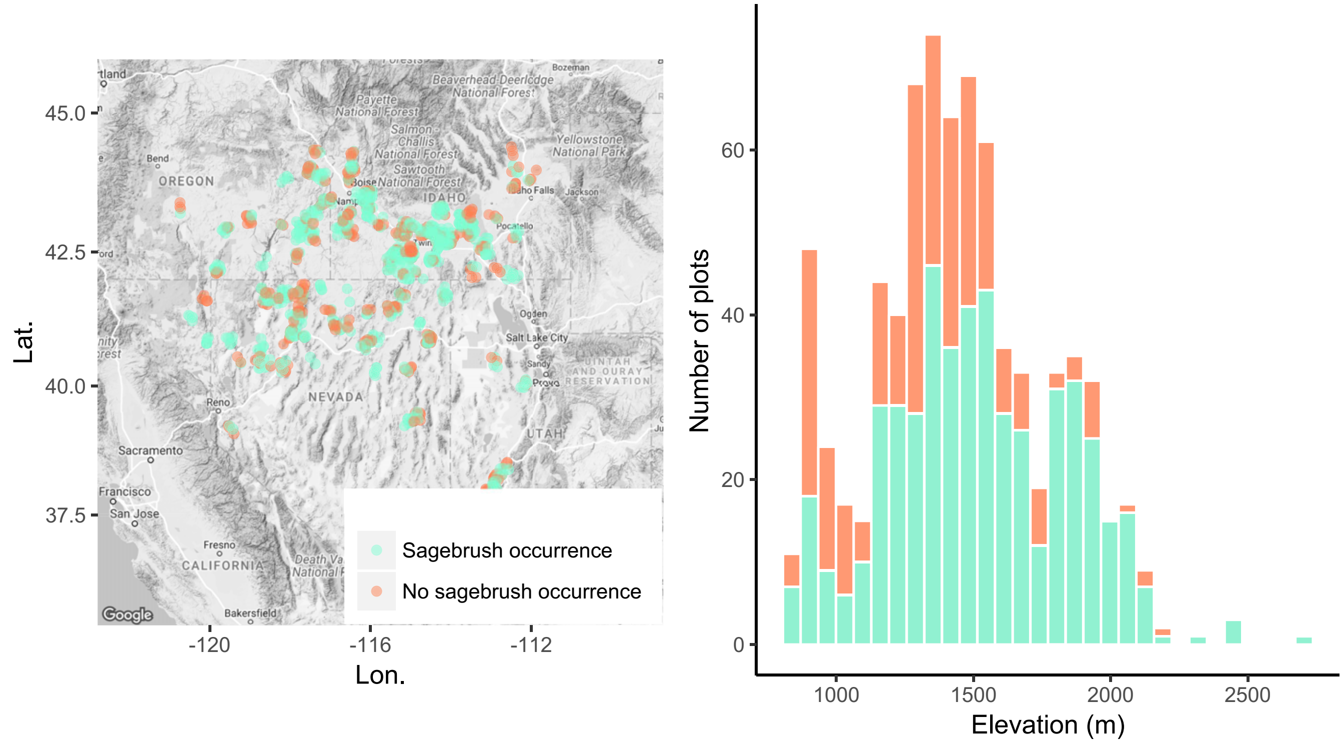

FIGURE 1 Geographic and elevational distribution (stacked histograms) of sampling plots across the Great Basin. Points on map are slightly jittered to make it easier to view nearby plots

moisture were minimal compared to environmental conditions, such as snowpack (Supporting Information Figure S7).

2.3 | Objective 1: Identifying conditions critical for sagebrush occurrence

To identify drivers of sagebrush occupancy, we compared precipitation, temperature, snow water equivalent (SWE; snowpack standardized by snow density), and soil moisture in the first growing season following seeding between plots with and without sagebrush occurrence. We calculated cumulative precipitation (rain and snow), average daily temperature, SWE, and soil moisture (volumetric water content), at 5-day intervals from the 1st to the 250th Julian day (1 January–7 September) of the year after seeding occurred (i.e., winter through the first summer). A 5-day interval reduced noise from day-to-day variability, but did not remove seasonal trends or change qualitative results from unsmoothed single day data. Because sagebrush has a very limited seed bank (~0%–10% seed viability near the soil surface 1 year after seeding; Wijayratne & Pyke, 2012), we are able to link weather and soil water dynamics in the first growing season after seeding that would have driven seedling establishment to restoration outcomes observed years later. We used a bootstrapping approach in R (R Core Team 2017) to infer differences between occurrence and nonoccurrence plots by subtracting 5,000 randomly drawn values from the mean and 95% confidence interval in nonoccurrence plots from occurrence plots. We did this for cumulative precipitation, average daily temperature, SWE, and soil moisture for each 5-day period.

2.4 | Objective 2: Quantifying the impact of environmental conditions on occurrence

We fit a Bayesian model to quantify the probability of sagebrush establishment in response to environmental variables in the year following seeding. The full model was

$$y_{it} \sim Bernoulli(p_{it})$$

$$logit(p_{it}) = \beta_0 + \beta_1\tau_{it} + \beta_2\rho_{it} + \beta_3\varphi_{it} + \beta_4\phi_{it} + \beta_5\omega_{it}$$

where y_{it} is the observed occurrence or nonoccurrence of sagebrush in plot *i* after seeding in year *t*, and *p* is the probability of establishment. Covariates in the model included: (a) τ_{it}, mean temperature from day 1 to 250; (b) ρ_{it}, cumulative precipitation through day 250; (c) φ_{it}, max winter SWE; (d) φ_{it}, mean soil moisture from day 70 to 100 in the top soil layer (0–5 cm) (identified in objective 1); and (e) ω_{it}, frost exposure, the number of 5-day periods with average minimum temperatures below 0° C and no snowpack over the first growing year. β parameters are inferred using noninformative priors *Normal* (μ = 0, σ^2 = 100). Models were fit in RJAGS (Plummer, 2003; R Core Team 2017), and we selected the most parsimonious model from every combination of these five variables using deviance information criterion (DIC). Because, our primary goal was to identify the weather condition directly following seeding that best promote sagebrush establishment, we only consider weather conditions in the first growing season following seeding, and not average plot or site-level conditions. However, as we illustrate in Figure 3e, we are also able to use this approach to recover valuable information on what plots are likely to reliably support establishment, and those that are not.

2.5 | Objective 3: Improving adaptive management strategies

Using the most parsimonious model (objective 2), we then assessed (a) how much anticipatory seeding can improve the probability of sagebrush establishment (i.e., the occurrence of one or more sagebrush plants in a plot); and (b) how recurring seeding over multiple years could improve the likelihood of successfully establishing sagebrush in plots. To address question 1, we calculated the mean, the inner 50% quantile, and the full range of annual sagebrush establishment probabilities using temperature and soil moisture data from 1979 to 2016. These calculations used only the year 1 vegetation scenario (see Ecohydrological modeling) and mean posterior parameter estimates. The distribution of annual establishment probabilities for each plot provides an estimate of how much targeted seeding for the "best" weather conditions in the recent past could have improved outcomes over the typical year's weather conditions in the same period. Using only mean parameter estimates allows us to explore the effect of interannual weather variability on sagebrush establishment while controlling for effects that other sources of variability or uncertainty (i.e., parameter uncertainty) could have on predictions. To address question 2, we simulated sagebrush establishment, assuming seeding occurred over five consecutive years, using temperature and soil moisture conditions in each of the 5 years following the initial seeding, and full posterior parameter estimates (i.e., parameter uncertainty). The annual conditions include effects of weather variability and vegetation recovery on soil moisture following fire (see Ecohydrological modeling). We then calculated the cumulative proportion of plots (excluding the nonrandomly selected sites) where the model predicted any sagebrush established (at least one sagebrush individual) after every seeding year. For example, the proportion of plots where establishment had occurred by year 3 include plots where establishment occurred in year 1 or 2 or 3 (see Supporting Information for more detailed description of calculations).

3 | RESULTS

3.1 | Objective 1: Identifying conditions critical for sagebrush occurrence

Temperatures were nearly 2°C cooler (Figure 2a,b) and the SWE in snowpack was nearly twice as high on average in the first growing season in plots where sagebrush occurred (Figure 2e,f). We observed no specific seasonal difference in precipitation amount (snow and rain) between occurrence and nonoccurrence plots (Figure 2c), although plots with sagebrush did have consistently higher cumulative precipitation, but were only significantly higher (7.2%, $p < 0.05$, Figure 2d) nearing the end of the summer (DOY 250, September 7th). Plots where sagebrush did not occur saw a more rapid decline in spring soil moisture at 0–5 cm soil depth, resulting in a large deficit from mid-March to mid-April (DOY 70–100) compared to plots where sagebrush did occur (up to ~0.04 m^3/m^3, 20%–30% less) (Figure 2g,h). Soil moisture differences between plots with and without sagebrush occurrence remained near zero for the remainder of the summer. The same spring soil moisture deficit extended, although somewhat dampened, to 5–10 cm of soil, but was not significantly present at deeper soil layers (>10 cm) (Supporting Information Figure S1).

3.2 | Objective 2: Quantifying the impact of environmental conditions on sagebrush occurrence

The most parsimonious model according to DIC included effects of mean temperature and spring soil moisture (see Supporting Information Table S1 for full DIC results). Spring soil moisture (β_4 = 2.499; 0.421–4.606 95% CI) had positive effects on the probability of occurrence, while increasing temperature (β_1 = −0.289; −0.394 to −0.184 95% CI) had a negative effect (Figure 3a,b). The top three models all included effects of temperature and soil moisture, but the second and third place models (which were within 1 DIC point) also included effects of maximum SWE and frost exposure, respectively. Although we found that sagebrush occurrence was positively related to SWE and precipitation, and negatively related to frost exposure, these variables were not selected by DIC to be included in the final model.

3.3 | Objective 3: Improving adaptive management strategies

The average annual probability of establishment (defined here as occurrence of at least a single big sagebrush plant) from 1979 to 2016 ranged from ~45% to 90% across all plots (Figure 3d). The single "best" seeding year in each plot (i.e., highest probability) ranged from ~65% to near 100% probability of establishment, and the maximum establishment probability at 31% of plots never exceeded 80%, particularly at low-elevation plots (Figure 3d). This indicated that the outcomes of seeding are likely to still be somewhat uncertain at lower elevation plots with chronic high temperatures and low soil moisture, even in their best years (Figure 3d). Still, simulations of repeated seeding over multiple years suggest that the total proportion of plots, where sagebrush occurs can increase to near 95% with 3–4 consecutive years of seeding (Figure 3c).

4 | DISCUSSION

The increased prevalence of fire, invasive species, and other anthropogenic disturbances have led to changes in dryland ecosystems worldwide (D'Antonio & Vitousek, 1992), including the sagebrush steppe (Balch et al., 2013; Pilliod, Welty, & Arkle, 2017). Because of the critical role that shrubs play structurally and functionally worldwide (West, 1983) and that sagebrush plays as a foundational species in shrub steppe ecosystems in western North America, efforts

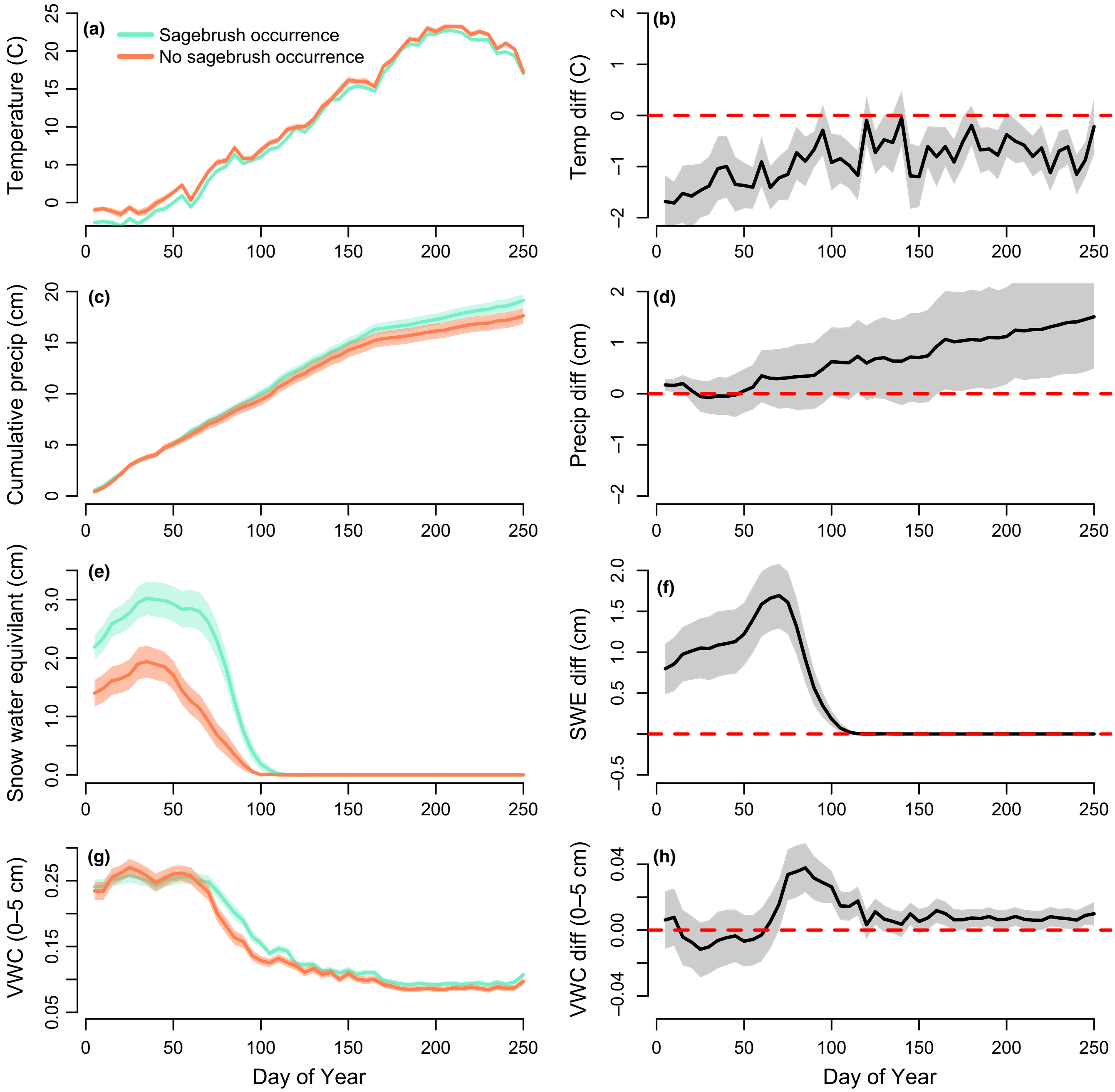

FIGURE 2 Seasonal dynamics of temperature (°C) (a,b), cumulative precipitation (cm) (c,d), snow water equivalent (cm) (e,f), and soil moisture from 0 to 5 cm depth (g,f) the year after seeding. Plots in the left column depict raw values averaged over all sites in the growing season following seeding, while the right column is the bootstrapped difference between the mean of plots with and without sagebrush occurrence. Shaded regions are the 95% CI, and the dashed red line indicates zero difference

to restore shrubs in general and sagebrush specifically have received significant investments (Copeland et al., 2018; Pilliod, Welty, & Toevs, 2017). However, our results suggest that the large interannual environmental variability inherent in these dryland sites (Pilliod, Welty, & Arkle, 2017) lead to conditions in which restoration treatments may be unlikely to support sagebrush establishment in any single year. This variability in part explains why efforts to promote sagebrush recovery, and the recovery of dryland perennial plants more generally, are often only marginally successful (Arkle et al., 2014; James, Svejcar, & Rinella, 2011; Knutson et al., 2014). Nonetheless, our results also suggest that adaptive seeding, and in particular repeated seeding when the ability to predict weather and outcomes is limited, may be powerful strategies to address persistent challenges and failures of one-time seeding approaches in dryland ecosystems (Menz, Dixon, & Hobbs, 2013; Vallejo, 2009).

We found that low temperatures and high spring soil moisture promote successful establishment of sagebrush across its range in the Great Basin. However, despite the importance of soil moisture,

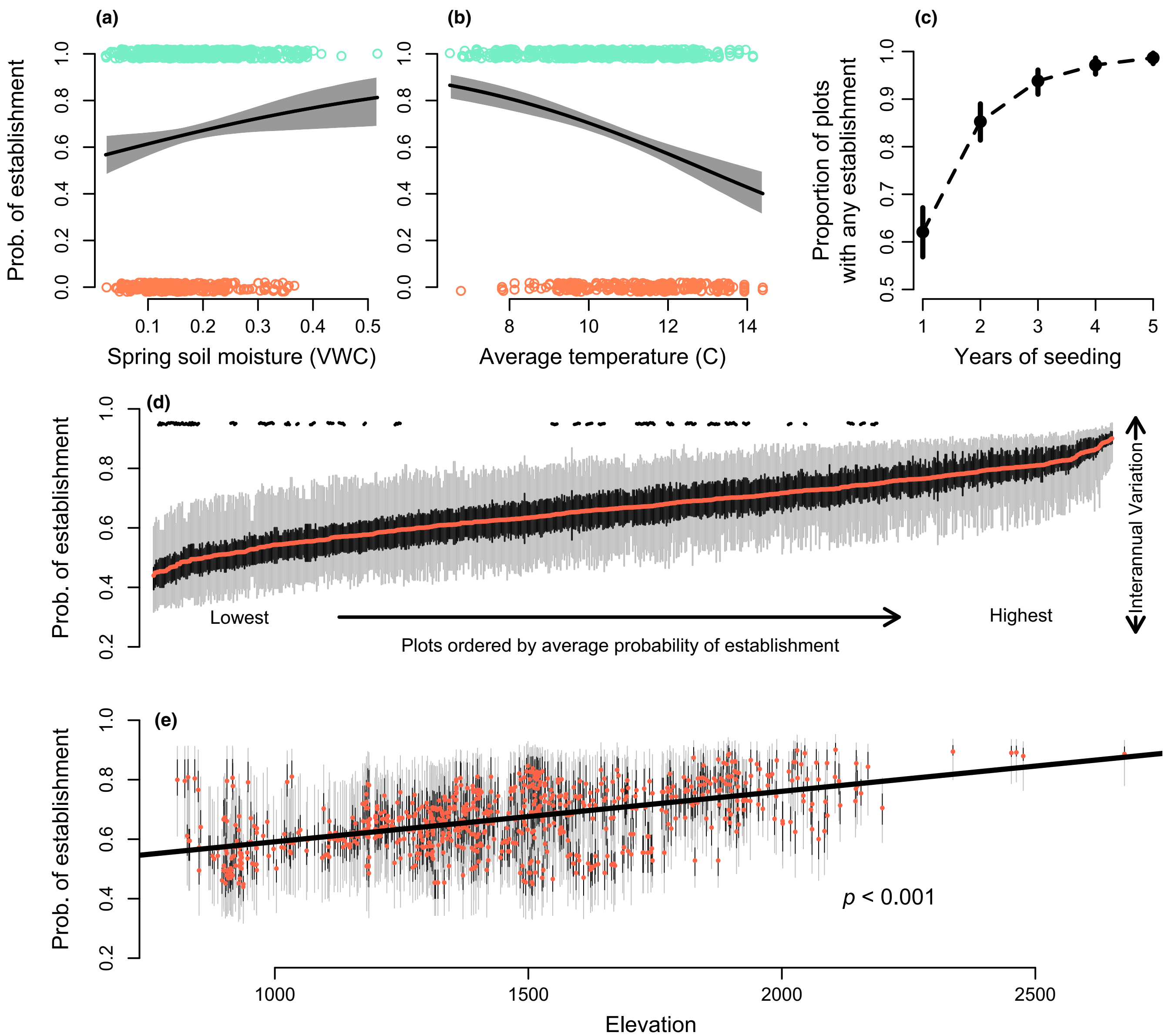

FIGURE 3 Drivers of sagebrush establishment and implications for adaptive management. Probability of establishment as a function of (a) spring soil moisture and (b) average temperature. Gray region is the 95% CI and points show data used to fit the model. (c) Total proportion of sites where establishment is predicted to occur after 1–5 years of seeding based on simulation with temperature and spring soil moisture conditions. Only randomly selected plots are included. (d) Distribution of annual establishment probabilities based on temperature and soil moisture conditions from 1979 to 2016 for each plot. Plots are rank ordered by average probability of establishment (red). Black region depicts the inner 50% quantile, and gray represents the full range on probabilities. Dots near top indicate nonrandom plots that were selected by the Bureau of Land Management. (e) Relationship between a plots elevation and average probability of establishment from 1979 to 2016, and regression between average annual probability of establishment (red points) and elevation. Error bars are the same as panel (d) [Colour figure can be viewed at wileyonlinelibrary.com]

total precipitation alone was a weak predictor. We hypothesize that part of the strong observed effect that temperature has in driving sagebrush dynamics (e.g., Renwick et al., 2018) is in altering the way in which precipitation is delivered (snow vs. rain), leading to cascading ecohydrological and ecological effects well beyond any effect of total amount of precipitation (Schlaepfer, Lauenroth, & Bradford, 2012b; Tietjen et al., 2017). Snowmelt allows for extended release of water into soil in spring months and limits evapotranspiration (Loik et al., 2004), potentially providing a more consistent source of moisture for plant germination and growth than rainfall. Andrus et al. (2018) similarly found the availability of cool temperatures and snowpack played a critical role in driving soil moisture and episodic establishment of spruce and fir species in the southern Rocky Mountains. Structural equation modeling of our data supports this hypothesis, indicating significant indirect effects of temperature through its effect on snowpack and soil moisture (Supporting Information Figure S2). This underscores that effects of environmental variation on ecological processes, including restoration, will often depend on interactions in climate variables that may not be reflected in aggregate climate metrics (Shriver, 2016).

Although our analysis focused on environmental conditions and identified temperature and soil moisture as dominant abiotic drivers of sagebrush establishment, biotic interactions can also influence restoration success. In particular, invasive annual grasses have dramatic impact on 1st-year postfire sagebrush establishment (Germino et al., in press) and vegetation dynamics in sagebrush plant communities (D'Antonio & Vitousek, 1992) and alternative seed mixes (e.g., native vs. nonnative perennial grasses) can influence the strength of competition with perennial grasses, regulating plant establishment on a site-by-site level (Barr, Jonas, & Paschke, 2017). Although seeding method could also influence the outcomes of seeding, Knutson et al. (2014) found no overall difference in long-term sagebrush cover between sites with drill and aerial seeding approaches (the most common seeding approaches in our dataset, Supporting Information Figure S6). Overall, our random sampling of BLM seeding applications and the wide spatio-temporal extent of our 771 plots indicate that weather plays a critical role in determining the success of sagebrush establishment. And, further analyses also indicate that wet conditions and cool temperatures in the first growing season are also associated with long-term outcomes in establishing high-density sagebrush stands (density ranged from 0 to 3.5 plants per m^2), perhaps indicating a positive feedback between conditions in the year of establishment and long-term density (Supporting Information Figures S4 and S5).

Ecologists increasingly recognize that climate change poses a major challenge for restoration (Butterfield, Copeland, Munson, Roybal, & Wood, 2017; Harris, Hobbs, Higgs, & Aronson, 2006). However, enabling restoration in warmer and increasingly variable climates will require identifying key demographic transitions and environmental conditions driving species, such as sagebrush, so that intervention efforts can be planned to maximize success (Bradford et al., 2018; Hardegree et al., 2018). One of the most robust and consistent climate projections in the Great Basin is increasing temperatures which will lead to declines in snowpack, regardless of the effect on total precipitation (Collins et al., 2013; Palmquist et al., 2016a). Our results suggest that this increased warming and associated declines in snowpack and spring soil moisture are likely to exacerbate ongoing challenges in establishing perennial plants like sagebrush after fire. In addition, widespread predictions of increasing variability in weather conditions (Collins et al., 2013) are likely to compound this effect by reducing the likelihood that any given year will support regeneration.

4.1 | Management implications

Despite these challenges, our results also suggest opportunities for designing and implementing flexible management techniques to improve restoration success and adapt to an increasingly variable future (Higgs et al., 2018; Ross, Bernhardt, Doyle, & Heffernan, 2015). First, anticipatory seeding, based on short-term forecasts of favorable conditions, could improve the likelihood of seeding success. For example, seeding when conditions are favorable (cool/wet spring vs. average conditions), will increase maximum establishment probabilities by 10%–20%, to above 80%, in 69% of plots (Figure 3d,e). The increasing accuracy of midrange (i.e., monthly, seasonal) weather forecasting, particularly for snowpack (Kapnick et al., 2018), is likely to make weather-targeted seeding an increasingly viable option. Weather-targeted seeding could be particularly beneficial to dryland restoration in locations that generally have higher rates of seedling establishment, for example, high elevation sagebrush sites (Figure 3e), to avoid wasting resources in drought years when establishment is unlikely. Nonetheless, the timing of ideal weather conditions may be infrequent in many sites and not align with the urgent need to stabilize soil and reduce the risk of further establishment of invasive species. Also, prolonged delays in seeding sagebrush after fire may require treatments with herbicides to reduce competition by annual and perennial grasses. In contrast, seeding for multiple consecutive years, a method proposed by Chambers et al. (2014) for the least resilient and resistant sagebrush communities, appears likely to significantly increase the probability of sagebrush establishment (Figure 3c). And, this approach may be particularly effective at low elevations (Figure 3e). The proportion of plots with predicted sagebrush occurrence after 2 years of seeding is nearly 85%. Translating our spatial results on restoration outcomes to temporal dynamics within a plot requires assuming that the seeding years are independent other than the effects of weather. In addition, our focus here, and therefore our inference on what drivers are critical for restoration, was simply on the establishment of any sagebrush, and not the likelihood of returning to a preburn condition. Still, these results are supported by the limited number of empirical studies that have found that repeated seeding improves restoration success in arid and semi-arid ecosystems more than other management interventions such as competitor control or seed preparation (Davies et al., 2018; Wilson, Bakker, Christian, & Li, 2004).

Although anticipatory and repeated seeding are likely to be a valuable tool in diverse grassland, shrubland, and forest ecosystems with episodic regeneration (e.g., Andrus et al., 2018; Petrie et al., 2017), large-scale empirical evaluations of the efficacy of these techniques are still sorely needed. For example, retrospective analyses could include how well historic midrange weather forecasts (e.g., http://www.cpc.ncep.noaa.gov/products/predictions/90day) were able to predict past restoration outcomes. Going forward, paired experiments within a site where randomized plots can be seeded once directly after a fire, every year over a 5-year period, or only in years when weather conditions (e.g., snowpack) are predicted to be above average, could be particularly useful. Given the low rates of success in establishing sagebrush and many dryland native plants with current management policies and approaches, explicitly incorporating experimentation into restoration policy over large spatial areas is likely to only increase our knowledge about the efficacy of different approaches and improve outcomes.

We found that temperature and spring soil moisture exert strong control on the likelihood of sagebrush occurrence after seeding, but not precipitation amount per se. Predictions of increasing temperatures and diminished snowpack across the Great Basin with climate change will likely make restoration increasingly difficult in coming decades, but adaptive seeding strategies, including anticipatory seeding and repeated seeding, could be powerful tools to leverage the inherent variability in dryland ecosystems and improve outcomes.

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AUTHOR CONTRIBUTIONS

DSP, MJG, MCD, DAP, & JBB were the lead investigators on the Great Basin portion of the project. RSA, DSP, MJG, & DAP led the collection of field data with help from numerous field assistants. RSA and JLW managed the data and metadata. CMA performed ecohydrological simulations with help from RKS and JBB. RKS performed analysis and wrote the first draft with help from JBB. All authors contributed to initial manuscript conception and editing.

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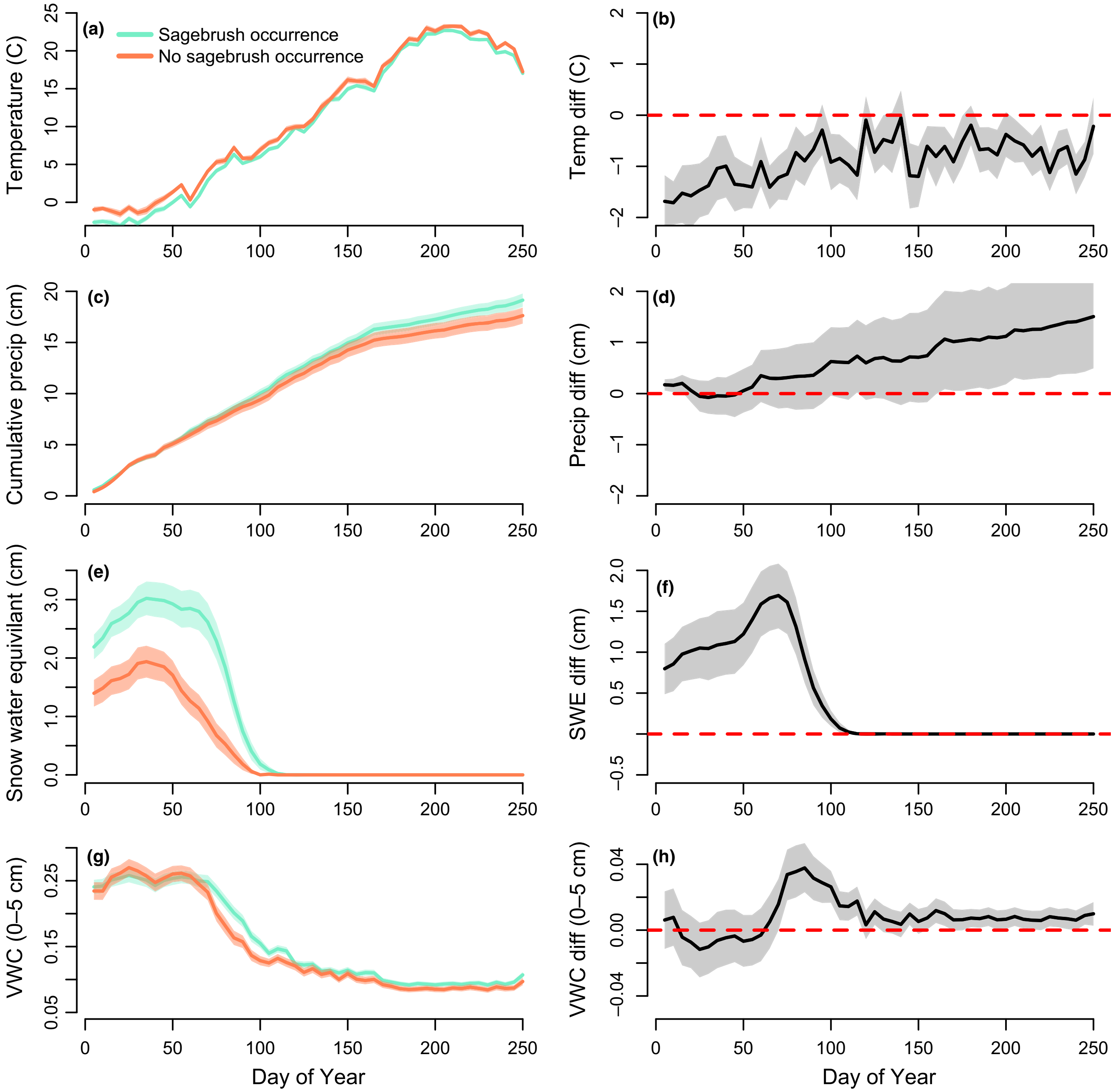

Restoration of native vegetation in dryland ecosystems, which encompass over 40% of terrestrial ecosystems, is a persistent and growing challenge. The sagebrush biome is a prime example of a pressing dryland restoration challenge for which success has been variable. Our results indicate big sagebrush occurrence after wildfire and seeding is most strongly associated with cool temperatures and wet soils, driven by abundant snowpack, in the first growing season. Adaptive management strategies that target seeding during cool, wet years, or mitigate effects of variability through repeated seeding may improve restoration outcomes in dryland ecosystems in the face of changing climate.